

Feeding strategy of an Early Miocene cetothere from the Toyama and Akeyo Formations, central Japan

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Abstract. The feeding strategy of cetothere from the Toyama and Akeyo Formations is discussed based on the mandibles of two individuals. Three synapomorphic characters in the mandible that are shared with balaenopterid whales (a laterally projecting coronoid process, a marked inward elevation at the dorsal edge of the ramus posterior to the coronoid process, and a sharply edged ventral margin on the middle part of the mandible) suggest that some cetotheres had already acquired an engulfment feeding mechanism by the late Early Miocene. Two other apomorphic characters (a quite high and elongated dorsal mandibular ridge and a ventrally well-projected mandibular angle) suggest robust development of the musculature of the mandible during the feeding process in the studied specimens in contrast to the weak development of the musculature in the balaenopterids. This may represent a primitive transitional stage of the engulfment feeding mechanism which could be related to the lack or poor development of highly elastic elements in the ventral pouch.

Key words: Cetotheriidae, Early Miocene, engulfment feeding, feeding mechanism, mandible, Mysticeti

Introduction

Mysticetes have acquired baleen plates and developed a unique filter feeding mechanism during the process of their evolution. The feeding strategy of the extant Mysticeti is generally divided into three types: skim feeding for plankton (Balaenidae), mud scooping (Eschrichtiidae), and engulfment feeding for fast-swimming krill and fish (Balaenopteridae) (Brodie, 1977; Pivovarov, 1979; Berta and Sumich, 1999). The evolution of filter feeding was a primary factor for the origin of mysticetes (Fordyce, 1980, 1989). Since the Cetotheriidae are the earliest true baleen-bearing, toothless mysticete family (Barnes, 1984; McLeod *et al.*, 1993; Fordyce and Barnes, 1994), the study of their feeding mechanism is important for considering the evolution of filter feeding in mysticetes. McLeod *et al.* (1993) pointed out that cetotheres have the following three morphological characteristics as compared with balaenopterids—(1) more posteriorly directed mandibular condyle; (2) larger coronoid process of mandible; and (3) longer zygomatic process of squamosal. Based on these characters, these authors briefly mentioned that cetotheres were probably engulfment feeders displaying a less specialized mandible and skull morphology and with a weaker throat groove than balaenopterids. However, there is no other detailed discussion in the literature about cetothere feeding

strategy.

Two cetothere mandibles were found from the Lower Miocene Toyama and Akeyo Formations, Gifu Prefecture, Japan. The mandible has a primary functional role for feeding, and its morphology may reflect to a high degree the feeding strategy. The purpose of this paper is to examine the feeding strategy of the cetotheres based on the two mandibles and to discuss the evolution of the engulfment feeding mechanism.

Materials

Two cetothere specimens were examined in this study. Both specimens are deposited in the Mizunami Fossil Museum, Mizunami, Gifu Prefecture, Japan (MFM).

MFM18124, Cetotheriidae gen. et sp. indet. (Figure 1).—Both mandibles, skull fragments, cervical and thoracic vertebrae, ribs, a sternum, a humerus, and some bone fragments. The right mandible is almost complete. This specimen was found from the Kubohara Facies of the Toyama Formation, Iwamura Group, Iwamura town, Ena County, Gifu Prefecture, Japan (Kimura *et al.*, 2000). The horizon from which this specimen was collected is correlated to the Maki Member of the Toyama Formation, Iwamura Group (Ujihara *et al.*, 1992). The Maki Member is assigned to the *Crucidentacula sawamurae* Zone (late

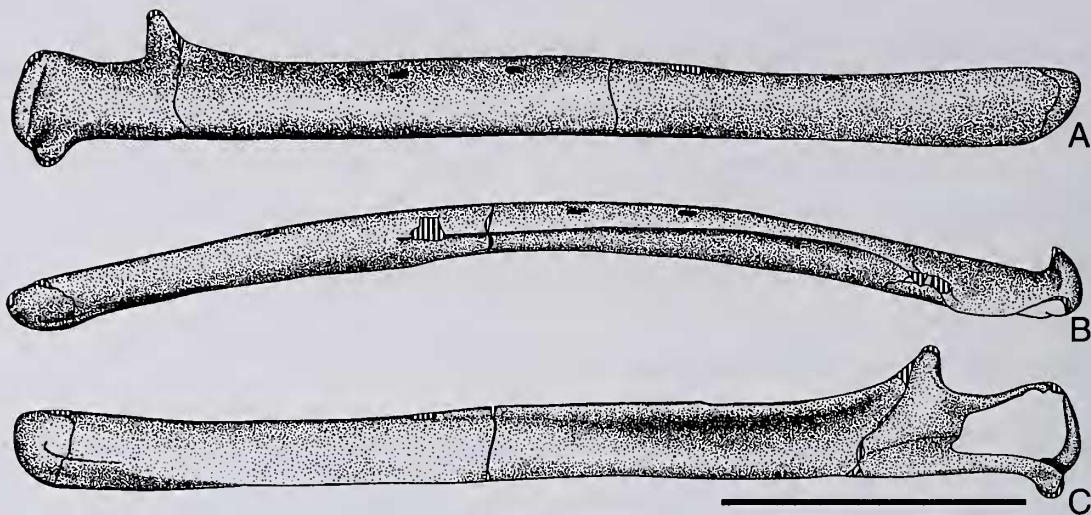


Figure 1. Cetotheriidae gen. et sp. indet. from Toyama Formation, MFM18124, right mandible. A. Lateral view. B. Dorsal view. C. Medial view. Hachures indicate areas where mandible is damaged. Scale bar equals 50 cm. After Kimura *et al.* (2000).

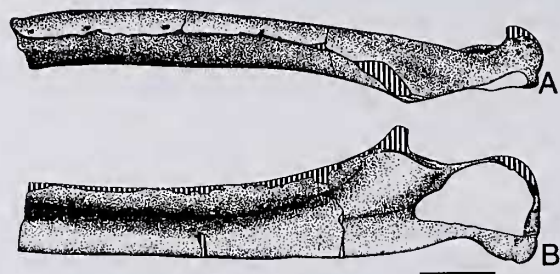


Figure 2. Cetotheriidae gen. et sp. indet. from Akeyo Formation, MFM18125, right mandible. A. Dorsal view. B. Medial view. Hachures indicate areas where mandible is damaged. Scale bar equals 10 cm.

Early Miocene: Barron and Gladenkov, 1995; Yanagisawa and Akiba, 1998) based on diatom biostratigraphy (Ito *et al.*, 1999). This specimen was originally described by Kimura *et al.* (2000).

MFM18125, *Cetotheriidae* gen. et sp. indet. (Figure 2). —Right mandible. A posterior half of the mandible including condyle and angle is preserved. This specimen was found from the Lower Miocene Yamanouchi Member, Akeyo Formation, Mizunami Group, Togari, Mizunami City, Gifu Prefecture, Japan and was once referred to *Mysticeti*, gen. and sp. indet. (Kamei and Okazaki, 1974: p. 283, pl.97, figs.6a, b). The Akeyo Formation consists of the Tsukiyoshi, Togari, Yamanouchi, and Hazama Members in ascending stratigraphic order (Itoigawa, 1974, 1980). Kobayashi (1989) estimated the age of the Akeyo Formation to be 17–17.5 Ma on the basis of fission-track dating. Itoigawa and Sibata (1992) suggested that the

Yamanouchi Member is assigned to Upper Zone N.7 to Lower Zone N.8 of Blow (1969). Kohno (2000) also suggested that the Yamanouchi Member is late Early Miocene (ca. 18–17 Ma) based on the radiolarian and diatom dating.

These two mandibles share a characteristic morphology of a quite high and elongated dorsal ridge with a concavity at its medial side. This character clearly distinguishes the present species from any other known mysticetes. These edentulous specimens are clearly distinct from primitive, toothed mysticete families. Additionally, these two mandibles are characterized by the following combination of characters: (1) a large mandibular foramen; (2) a well-developed coronoid process that projects dorsally, laterally, and posteriorly; (3) a posteriorly directed articular surface of the condyle; (4) a sharply edged ventral margin on the middle part of the mandible. This combination of characters is not found in any extant mysticete families (*Balaenopteridae*, *Eschrichtiidae*, *Balaenidae*, and *Neobalaenidae*). Therefore, these two specimens are recognized as the same species in the *Cetotheriidae*, gen. and sp. indet. as will be discussed below (Kimura *et al.*, 2000). The *Cetotheriidae* have long been considered as a paraphyletic grade lacking the diagnostic characters of more derived mysticete families (e.g., Fordyce and Barnes, 1994).

For comparison, I examined the material of the following extant *Mysticeti* housed in the National Science Museum, Tokyo (NSMT): *Balaenopteridae*: *B. acutorostrata* (NSMT-M15941, NSMT-M32543), *B. edeni* (NSMT-M03538, NSMT-M32599); *Eschrichtiidae*: *E. robustus* (NSMT-M15940); *Balaenidae*: *B. glacialis* (NSMT-M03538).

Table 1. Measurements of right mandible (in mm), Cetotheriidae gen. et sp. indet. from Toyama (MFM18124) and Akeyo (MFM18125) Formations.

	MFM18124	MFM18125		
Length of mandible in a straight line	1777	734+		
Length of mandible along outside curvature	1810	735+		
Distance from anterior end of ramus to level of center of coronoid process along outside curvature	1572	—		
Vertical diameter through coronoid process	214+	154+		
Vertical diameter of hinder end of ramus including condyle	187+	152+		
Transverse diameter of condyle	108+	80+		
Vertical (H) and bransverse (W) diameter in 100-mm increments form the anterior end of ramus				
	H	W	H	W
100	140	49	104+	63
200	132	53	105	65
300	123	59	113	64
400	117	65	119+	72
500	121	68	154+	71
600	121	70	107	55
700	123+	73		
800	132	74		
900	132	75		
100	135	78		
1000	136	80		
1100	136	80		
1200	138	72		
1300	147	78		
1400	172+	85		
1500	133	84		
1600	145	71		
1700				

Description

The right mandible of MFM18124 is almost complete except for erosion of an angle (an), a dorsolateral edge of a coronoid process (cp), and a dorsal and lateral part of a condyle (co) (Figure 1). All of the epiphyses on the preserved vertebrae (cervical and thoracic) are firmly ankylosed to the centra, and this condition in extant mysticetes is regarded as evidence of physical maturity (Omura, 1975). MFM18125 consists of only the posterior half of a right mandible and is smaller than MFM18124 by approximately 75% (Table 1). In MFM18125, the coronoid process is broken off except for its base and the dorsal and lateral portion of the condyle was eroded away (Figure 2). Unless otherwise mentioned, the descriptions

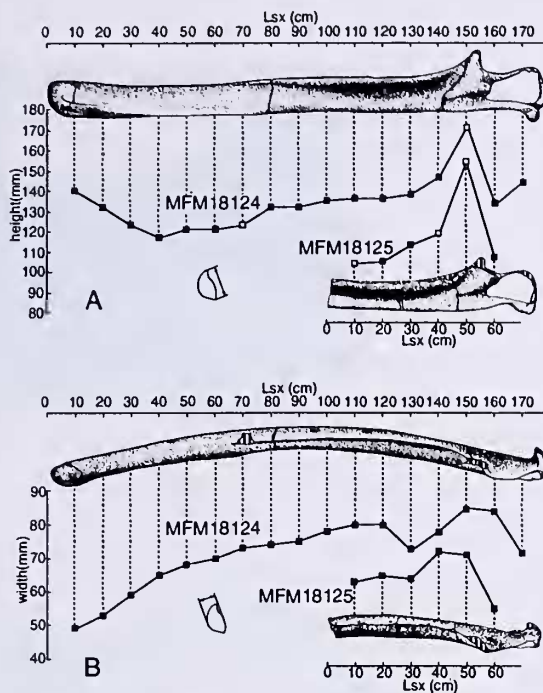


Figure 3. Change in measurements. A, B. Height (A) and width (B) of right mandible of MFM18124 and MFM18125 in 100-mm increments from anterior end, at left. Open squares represent minimum values, owing to breakage of specimen. Abbreviations: Lsx, distance between anterior end of ramus and measurement points along a straight line. Modified from Kimura *et al.* (2000).

are based on MFM18124.

A roughened area at the anterior tip of the mandible is short and does not exceed 75 mm. A longitudinal crease on the medial surface at the anterior tip of the mandible is 142 mm long. The horizontal ramus is rotated around its axis and its medial surface slopes lingually. The amount of rotation at the anterior tip of the horizontal ramus is about 30° against the medial surface at the region of the coronoid process. The horizontal ramus tapers slightly in dorsoventral diameter from the region of the coronoid process toward the anterior tip (Figure 3). However, the dorsoventral diameter increases at the anterior one-fifth of the mandible.

MFM18124 preserves three mental foramina along the dorsolateral surface of the mandible. These foramina occur at 485, 1010, and 1199 mm behind the anterior tip of the mandible and lie at 7, 31, and 43 mm below the dorsal margin of the horizontal ramus. These foramina open into an anteriorly directed groove.

Figure 4 shows the cross sections of the mandibles. There is a noticeable flattening of the anterior one-third of the medial surface of the mandible. Posterior to this, the medial surface of the ramus becomes convex medially. A concavity occurs at the medial side of the high dorsal ridge.

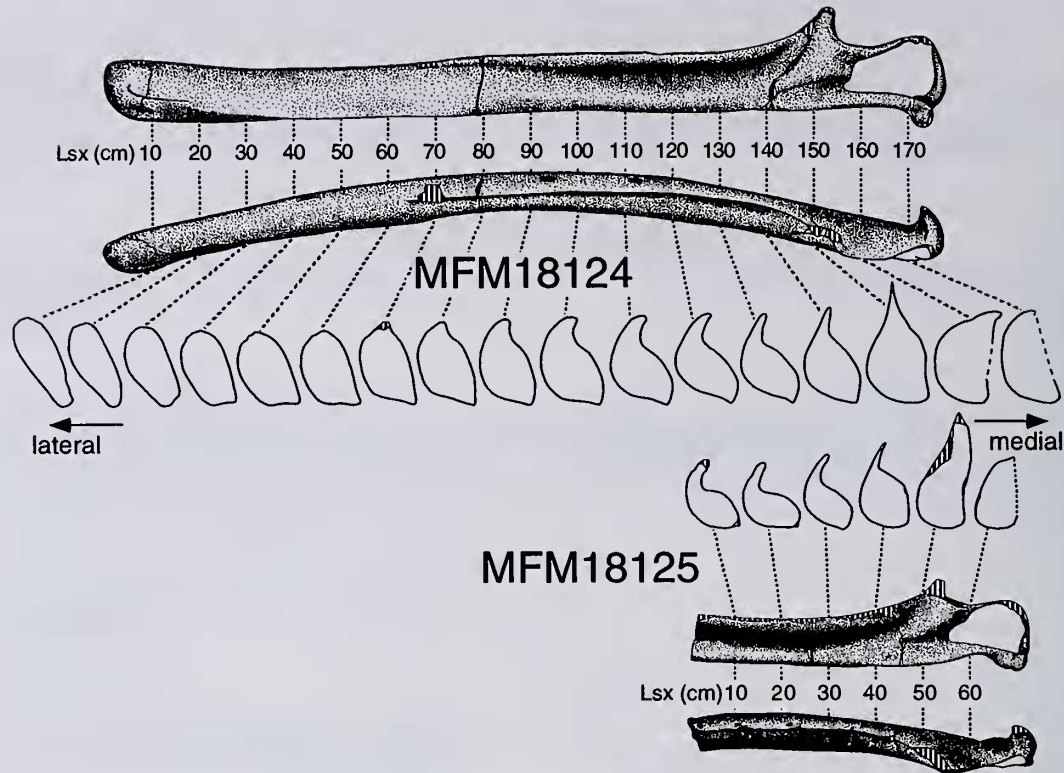


Figure 4. Cross sections of right mandible of MFM18124 (above) and MFM18125 (below). Hachures indicate areas where mandible is damaged. Dashed line in cross section represents mandibular foramen. Abbreviation: Lsx, distance between anterior end of ramus and measurement point along a straight line.

A groove is present on the medial surface of the horizontal ramus anterior to the mandibular foramen (mf). The lateral surface of the mandible becomes progressively convex dorsoventrally toward the posterior end. The greatest transverse diameter is below the midline at the middle part of the mandible. Further posteriorly, the greatest diameter shifts dorsally. Ventrally the lateral surface meets the medial surface to form a well-defined angular edge in the middle part of the mandible. This angular edge approaches the internal face anteriorly. The angular edge becomes rounded posteriorly at the region of the coronoid process.

In dorsal view, the mandible is only slightly bowed laterally (Figure 1B). The length of the mandible along the outside curvature represents only 102% of the length of the mandible in a straight line. The outward curvature is gradual and not abruptly flexed. There is no reflexion at the region of the coronoid process as in the balaenopterids. In lateral view, the ventral profile of the horizontal ramus is almost straight (Figure 1C). But in MFM18125, the ventral margin of the mandible anterior and posterior to the coronoid process is dorsally arched (Figure 2B).

The coronoid process projects dorsally, posteriorly, and laterally. The apex of the coronoid process is located at

87% of the length of the mandible along the outside curvature from the anterior extremity. The anterior margin of the coronoid process rises gradually, but its posterior margin descends abruptly. A shallow concavity occurs on the medial surface of the coronoid process along its anterior margin (Figure 5). Behind the apex, the posterior edge of the coronoid process thickens whereas the anterior edge remains thin. An inward elevation (ie) occurs on the medial surface of the upper border near the middle of the ramus behind the coronoid process (Figure 5). The inward elevation has a sharp edge and projects inward. It becomes more prominent anteriorly. This inward elevation continues anteriorly and dorsally to a ridge on the medial surface of the coronoid process. In MFM18125, because of breakage, a longitudinal groove occurs at a dorsomedial edge of the corresponding part of the ramus. But the remaining part projects slightly medially, and this suggests the development of the inward elevation in MFM18125. The inward elevation is also found in the Balaenopteridae. However, the elevation in the Balaenopteridae is more rounded than that of MFM18124 and MFM18125 (personal observation). For a distance of at least 880 mm anterior to the apex of the coronoid process, a relatively high dorsal

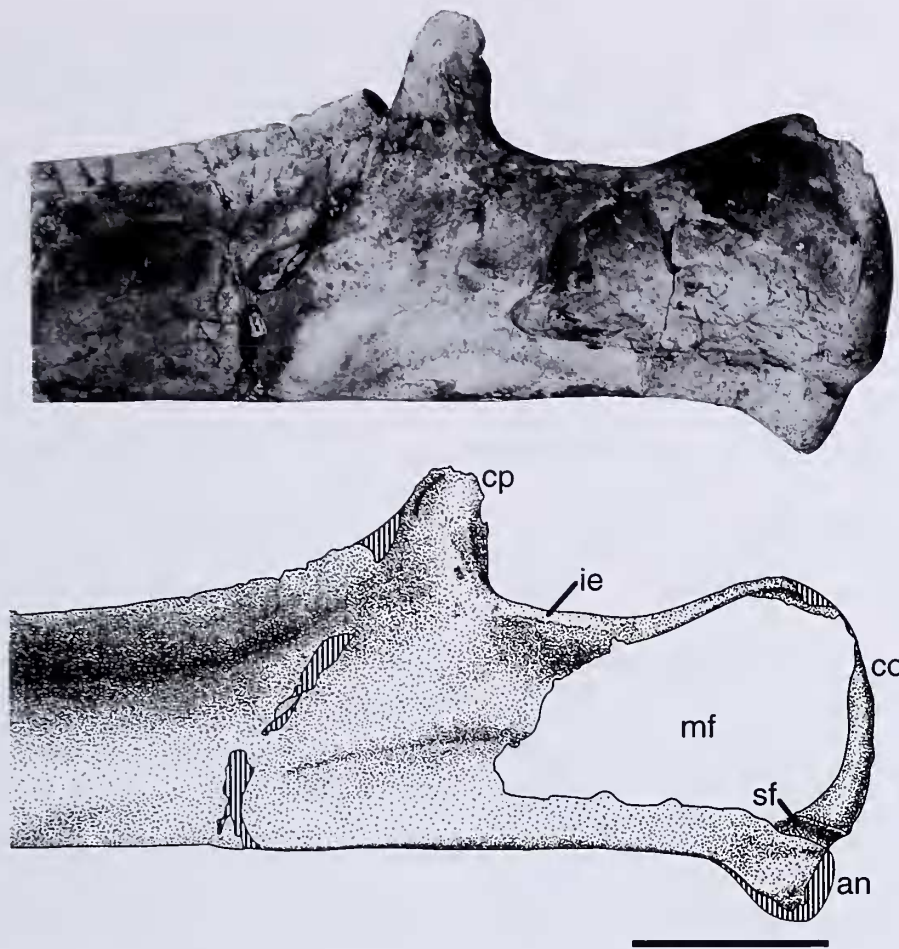


Figure 5. Cetotheriidae gen. et sp. indet. from Toyama Formation, MFM18124. A, B. photograph and drawing of posterior part of right mandible, medial view. Hachures indicate areas where mandible is damaged. Abbreviations: an, angle; co, condyle; cp, coronoid process; ie, inward elevation; mf, mandibular foramen; sf, subcondylar furrow. Scale bar equals 10 cm. Modified from Kimura *et al.* (2000).

ridge forms the dorsal edge of the horizontal ramus (Figures 1, 4). Anteriorly, the dorsal ridge becomes rounded and curved medially.

A mandibular foramen is large. The condyle is expanded from side to side and is more convex transversely than dorsoventrally. The forward-curving external border of the condyle projects beyond the lateral surface of the adjacent portion of the ramus. The maximum transverse expansion of the condyle (MFM18124, 108 mm+; MFM18125, 80 mm+) occurs below the midline of its vertical diameter. Ventrally, the condyle almost maintains its width. Ventrally, the condyle is bounded by a subcondylar furrow (sf) above the angle. This furrow extends across the posterior face of the condyle and decreases in depth laterally. Although the angle of MFM18124 is damaged, the preserved portion projects far ventrally. In MFM18125, the angle is almost complete, robust and projects ventrally (Figure 2).

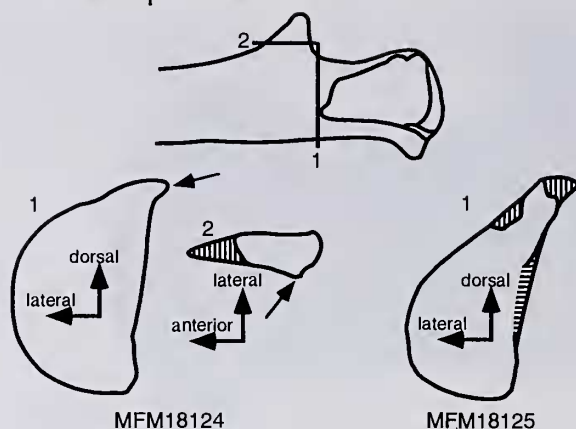
Discussion

Morphological characters of mysticetes can reflect their feeding strategy (McLeod *et al.*, 1993). Since the mandible plays an important role in feeding process, we can make inferences about the feeding strategy of fossil mysticetes from their mandibular morphology.

Apomorphies for engulfment feeding

Coronoid process.—The coronoid process of the mandible in the balaenopterids is large and projects both posteriorly and laterally. The coronoid process in the basal suborder Archaeoceti and the toothed mysticetes Aetiocetidae is also large, but does not project laterally (Kellogg, 1936; Barnes *et al.*, 1995; Gingerich and Uhen, 1996; Hulbert *et al.*, 1998). The laterally projected coronoid process of the balaenopterids is considered to be a derived condition. In contrast, the non-engulfment feed-

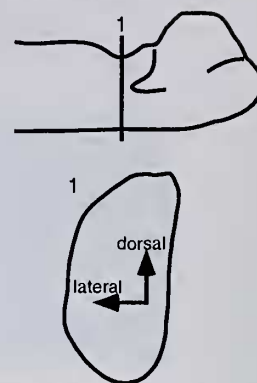
Studied Specimens



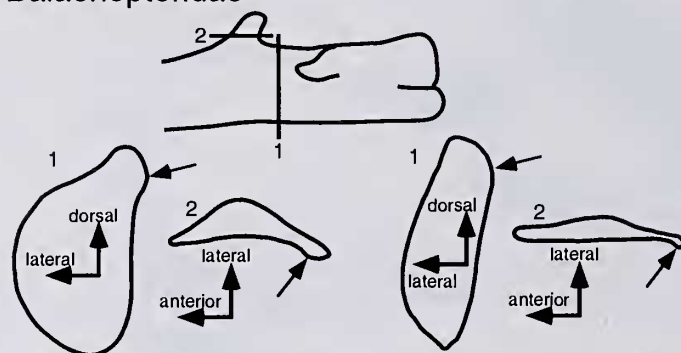
MFM18124

MFM18125

Eschrichtiidae

*E. robustus* (NSMT-M15940)

Balaenopteridae

*B. acutorostrata* (NSMT-M32543)*B. edeni* (NSMT-M32599)

Balaenidae

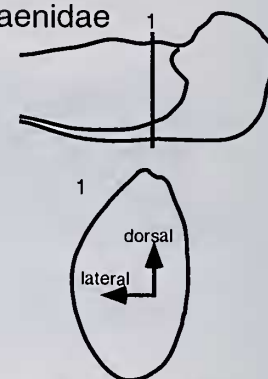
*B. glacialis* (NSMT-M05153)

Figure 6. Cross sections of mandible just behind (1) and base (2) of coronoid process (not to scale). Arrows indicate an inward elevation. Hachures indicate areas where mandible is damaged.

ers (Balaenidae, Neobalaenidae, and Eschrichtiidae) convergently acquired a quite small coronoid process (Barnes and McLeod, 1984) unless those three families form a monophyletic group.

The coronoid process provides the insertion for the temporal muscle which generates most of the elevating force during feeding in rorquals (Carte and MacAlister, 1868; Schulte, 1916; Lambertsen, 1983; Lambertsen *et al.*, 1995). The shape of the coronoid process is functionally important for engulfment feeding because it requires a complicated motion of the mandible (Lambertsen *et al.*, 1995). MFM18124 has a large and laterally projected coronoid process similar to the balaenopterids (Figures 1, 5). Although the coronoid process of MFM18125 is missing, the base of the process also suggests that the process is curved laterally (Figure 2B).

Ventral margin of the mandible.—The cross-sectional shape of the ventral margin of the middle part of the mandible is clearly differentiated among the mysticete families (Deméré, 1986; Nagasawa, 1994). In the Balaenopteridae,

the ventral margin of the cross section in the middle part of the mandible forms a well-defined angular edge (Deméré, 1986; Kimura *et al.*, 1987; Nagasawa, 1994). The sharply edged ventral margin of the cross section in the middle part of the mandible is also developed in MFM18124 and MFM18125. The mylohyoid muscle is attached along this ventral ridge (Pivorunas, 1977; Lambertsen, 1983). In engulfment feeding, the mylohyoid muscle, together with other muscles (multiple muscle layers: Lambertsen, 1983), plays an important role in expelling the sea water through the baleen plates (Lambertsen, 1983; Orton and Brodie, 1987). The marked ridge on the ventral margin of the mandible suggests the presence of well-developed mylohyoid muscles.

Inward elevation of the mandible.—The degree of development of the elevation is variable in the Balaenopteridae, stronger in *B. acutorostrata* than in *B. edeni* (Figure 6). This inward elevation is also found in *B. musculus* (Struthers, 1889). In *Megaptera novaeangliae*, the elevation rises upward on the same part of the mandible and

is called the post-coronoid elevation (Struthers, 1889). The studied specimens have a remarkable inward elevation on the medial surface of the upper border near the middle of the ramus behind the coronoid process similar to the balaenopterids.

In contrast, the structure of the corresponding part is quite different in the Eschrichtiidae and Balaenidae. In the Eschrichtiidae, the coronoid process is quite low and projects laterally. Posterior to the coronoid process, there is a low process which projects dorsally, and this process continues posteriorly to a low ridge on the medial surface of the ramus. Below this low ridge, another longitudinal faint ridge is also present. In the Balaenidae (*B. glacialis*), the coronoid process is faint and, posterior to the coronoid process, a shallow groove is present on the dorsomedial surface of the ramus (anteroposterior length of the groove: right 46 mm/left 59 mm). This groove makes a low bump on the medial surface of the upper part of the ramus. Although there is a ridge on the dorsomedial surface of the ramus in both families, the ridge is faint and does not project medially (Figure 6). Further, there is no ridge on the medial surface of their quite low coronoid process. Therefore, these structures found in the Eschrichtiidae and Balaenidae are clearly distinguished from the prominent inward elevation present in the studied species and the Balaenopteridae.

The frontomandibular stay is a functionally and anatomically specialized tendon of the temporal muscle and is attached to the inward elevation (Struthers, 1889; Lambertsen *et al.*, 1995). This stay apparatus is common among the balaenopterids and serves to support the motion of the mandible during the feeding process, especially in initiating engulfment (Lambertsen *et al.*, 1995).

The above three characters suggest that the species had an acquired engulfment feeding mechanism. The Cetotheriidae is believed to include taxa closely related to the ancestor of the Balaenopteridae (Fordyce and Barnes, 1994). The three apomorphies are also found in the Balaenopteridae. However the phylogenetic relationship between the cetothere species in this study and the Balaenopteridae is still unclear and the analysis of the relationship is beyond the scope of this study. So, more detailed consideration is needed to ascertain whether these characters are synapomorphies between the two.

Efficiency of engulfment feeding

One aspect of engulfment feeding efficiency relates to the size of the mouth cavity. The mandible of the studied specimens is slightly curved, a primitive condition (Barnes and McLeod, 1984). Deméré (1986) suggested that the width of the rostrum is directly proportional to the extent of the lateral curvature of the mandible. This suggests that the mouth cavity of the studied specimens was relatively

small and that engulfment feeding in MFM18124 and MFM18125 was less efficient than in the extant balaenopterids.

The mandible of the balaenopterids changes continuously in its position during the engulfment feeding process by three motions—(1) alpha rotation: an inward and outward rotation around the longitudinal axis of the mandible; (2) delta rotation: depression and elevation of the mandible; and (3) omega rotation: medial and lateral movement of a condyle of the mandible (Lambertsen *et al.*, 1995). The temporomandibular articulation in extant balaenopterids is, unlike other mammals, composed of a fibrous meniscus infiltrated with oil (Hunter, 1787; Carte and MacAlister, 1868; Beauregard, 1882; Beneden, 1882; Struthers, 1889; Schulte, 1916). Since this meniscus enables the movement of articulation more effectively, like planar quadrilateral connecting system, the squamomandibular articulation of the balaenopterids can perform its complicated movements (Lambertsen *et al.*, 1995). Cetotheres are generally characterized by having a more or less flattened articular surface of the squamosal (Miller, 1923). This suggests that the temporomandibular articulation composed of a fibrous meniscus was not acquired or poorly developed in the Cetotheriidae. Neither of the studied specimens includes the squamosal, and it is unclear that they were able to perform these complicated movements of the mandible.

Lambertsen *et al.* (1995) suggested that stronger lateral curvature and elongation of the mandible would increase alpha-rotation of the mandible. If these specimens were able to perform alpha-rotation, the small amount of curvature suggests that this could not contribute greatly to the enlargements of the mouth. This suggests that cetotheres fed less efficiently than the balaenopterids.

Feeding strategy of Balaenopteridae

In the Balaenopteridae, the musculature of the mandible mainly braces the jaw during engulfment feeding and does not actively open it (Lambertsen, 1983; Orton and Brodie, 1987; Lambertsen *et al.*, 1995). This passive movement of the mandible is mainly caused by water pressure resulting from locomotion and allied action of a ventral pouch (Brodie, 1977; Orton and Brodie, 1987; Lambertsen *et al.*, 1995; Bakker *et al.*, 1997). The ventral pouch (body wall below the cavum ventrale; Lambertsen, 1983) is a highly elastic grooved structure which consists mainly of blubber and multiple muscle layers, covering the ventral surface of the whale from the anterior border of the mandible to the umbilicus or further (Pivorunas, 1979; Lambertsen, 1983; Orton and Brodie, 1987). The pouch is filled by voluntary increase of the curvature of its elastic ventral wall by contraction of multiple muscle layers. This changes the water flow between the upper and lower surface of the head and causes asymmetry of the hydraulic pressure which assists in

depressing the mandible (Bernoulli principle) (Lambertsen *et al.*, 1995). The passive movement of the mandible in filling the pouch is also suggested by the fact that the relaxation of jaw musculature makes the lower jaw drop (Lambertsen, 1983). Lambertsen *et al.* (1995) also suggested that as a result of the mode of attachment of the ventral pouch to the mandible, hydraulic pressure can rotate the mandible around its longitudinal axis (alpha rotation). Active contraction of musculature is required for water expulsion, especially in the final phase (Lambertsen, 1983; Orton and Brodie, 1987). Orton and Brodie (1987) suggested two sources for passive motion of the mandible in expulsion and these are accompanied with changes in swimming speed. They are based on a recoil of hydraulic pressure and resiliency of elastic elements of the ventral pouch. In addition, when the whale ceases propulsive action, the energy of the frontomandibular stay against the water flow is released and the stored energy of the stay assists closure of the mouth (Lambertsen *et al.*, 1995).

Therefore, we can summarize the source for the efficient feeding mechanism of the Balaenopteridae as follows: (1) the strong development of the highly elastic elements in the ventral pouch; (2) the multiple muscle layers which serve to deepen the oral cavity; (3) the frontomandibular stay.

Feeding strategy of studied specimens

The specimens studied display the aforementioned synapomorphies with the balaenopterids, but also show two apomorphic characters, which are clearly different from the Balaenopteridae. Both these characters suggest that engulfing is a more active muscular process than in the Balaenopteridae.

Dorsal ridge.—The specimens studied have a relatively high and elongated dorsal ridge with a concavity at its medial side (Figures 1, 2, 4). In MFM18124, there is a roughened area on most of the medial surface of the ridge. This area can be considered as the origin of the caudal part of the mylohyoid muscle. The mylohyoid muscle is only attached along the ventral border in the extant Mysticeti (*B. acutorostrata*: Pivorunas, 1977, Lambertsen, 1983; *B. borealis*: Schulte, 1916) and the extant Odontoceti (Reidenberg and Laitman, 1994) at the middle part of the mandible. But in ungulates, the muscle is separated into rostral and caudal parts, and the caudal part originates from the medial surface of the mandible just ventral to the alveolar border (Getty, 1975; Sisson, 1975; Nickel *et al.*, 1986). The close relationship between cetaceans and ungulates has been confirmed by much paleontological and molecular data (e.g., Van Valen, 1966; Shimamura *et al.*, 1997). It appears that cetotheres display the primitive ungulate muscle pattern; the dorsal ridge and allied concavity may indicate the area for the attachment of the mylohyoid muscle. Therefore,

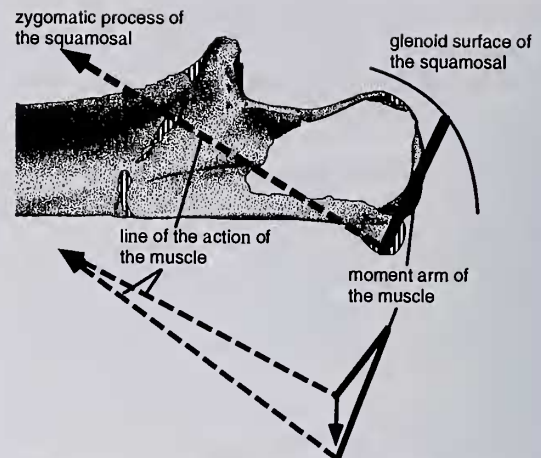


Figure 7. Schematic diagram showing moment arm of superficial portion of masseter muscle (above) and changing of moment arm caused by ventral projection of angle (below). Solid and dashed lines indicate moment arm of muscle and line of action of muscle, respectively.

the relatively high dorsal ridge with the well-developed concavity of the specimens studied suggests a highly developed mylohyoid muscle, unlike the balaenopterids.

The mylohyoid muscle is the largest muscle in the multiple muscle layers of the floor of the mouth. The multiple muscle layers of the ventral pouch are the primary contributor for active expulsion of water through the baleen (Lambertsen, 1983). In addition, at the final phase of water expulsion, the tongue is forced upwards by contraction of the mylohyoid muscle and this forcibly expels the remaining sea water through the baleen (Lambertsen, 1983). The mylohyoid muscle is primarily an elevator of the tongue (Yamaoka *et al.*, 1992). Thus, the development of the mylohyoid muscle suggests that the studied specimens required active musculature for water expulsion during feeding.

Angle.—The angle provides the insertion of the muscles for the movement of the mandibles, such as the medial pterygoid muscle, the digastricus muscle, and the superficial portion of the masseter muscle (Carte and MacAlister, 1868; Schulte, 1916; Lambertsen *et al.*, 1995). The angle of the specimens studied is large and projects ventrally (Figure 1, 2). This is clearly shown by the ratio of mandibular height through angle to mandibular length along outside curvature of the adult individual (converted to percentages): MFM18124 10.3+%; *B. acutorostrata* 8.5–9.5% (Turner, 1891–1892; Omura, 1975), *B. edeni* 7.9–9.2% (Omura *et al.*, 1981), *B. musculus* 8.3–9.3% (Struthers, 1889; Omura *et al.*, 1970), *B. borealis* 7.6–8.1% (Nishiwaki and Kasuya, 1971), *M. novaeangliae* 9.1% (Struthers, 1889). The ventrally projected angle implies that the area for the insertion of the muscle is also posi-

tioned ventrally. This would increase the moment arm of the superficial masseter and thus improve the mechanical advantage of the mandible (Herring and Herring, 1974; Vizcaíno and Bargo, 1998) (Figure 7). Therefore, the morphology of the angle suggests that the specimens studied could produce a more powerful motion of the mandible compared with the balaenopterids.

Both of these characters suggest the active contribution of the musculature of the mandible during feeding. This is in marked contrast to the passive contribution of the musculature of the mandible in the Balaenopteridae. The sources for the efficient feeding mechanism in the Balaenopteridae have been summarized above. In the specimens studied, the sharply edged ventral margin at the middle part of the mandible and the well-developed inward elevation indicates the development of the mylohyoid muscle and therefore the multiple muscle layers and frontomandibular stay, respectively. Therefore the robust contribution of the musculature of the specimens studied can be explained by the lack or poor development of the highly elastic elements in the ventral pouch.

Conclusion

I propose the following scenario of evolution of the engulfment feeding mechanism in baleen whales. Early mysticetes (aetiocetids) used filter feeding with teeth, and later cetotheres used baleen. Engulfment feeding was present in Cetotheriidae by the late Early Miocene. However, the feeding mechanism in the Early Miocene cetotheres required more active musculature than in the balaenopterids because of poor development or lack of the highly elastic elements in the ventral pouch. The well developed elastic elements in the skin are highly characteristic and are one of the key structures enabling passive movement of the mandible in the Balaenopteridae. The elastic elements evolved in the Balaenopteridae and enhanced efficiency of the mandible. In addition, balaenopterids have lost the apomorphic characters unrelated to the active musculature of the mandible during engulfment feeding. The feeding strategy suggested by the studied specimens may represent a primitive transitional stage of the evolution of the engulfment feeding mechanism.

The skull morphology may also exert an influence on the feeding mechanism (McLeod *et al.*, 1993). However, no skull was preserved in both specimens studied, except for a few fragments of the skull in MFM18124. Generally, cetotheres are characterized by primitive skull morphology. The apomorphic characters of the specimens studied which suggests more active contribution of the musculature of the mandible during the feeding process might not only be due to its feeding mechanism, but also to its primitive skull morphology. An additional specimen with a well-

preserved skull is needed to address the feeding strategy of the studied specimens in more detail.

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